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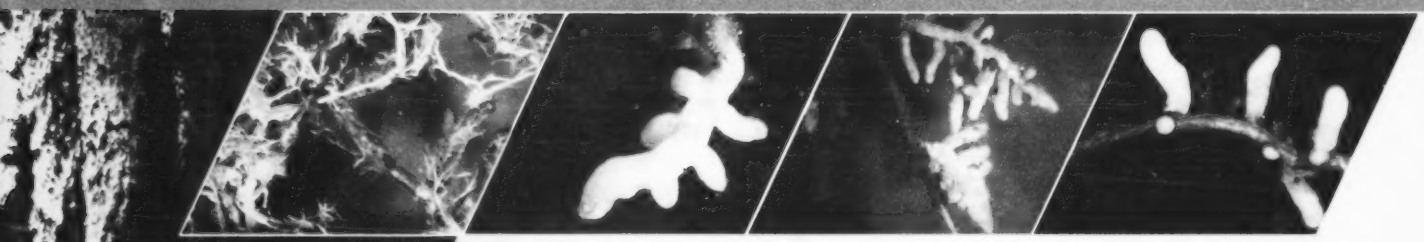
Re-establishment of ectomycorrhizae from refugia bordering regenerating Douglas-fir stands on Vancouver Island



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Abstract

The objective of this study was to determine the influence of refugia on the rate of recovery of ectomycorrhizae (EM) diversity in clearcut and replanted Douglas-fir *(Pseudotsuga menziesii)* forests in British Columbia, Canada. Transects were established at two locations on southern Vancouver Island: Northwest Bay and Koksilah. The transects extended from 15 m inside the remaining 90(+)-year-old (mature) or old-growth Douglas-fir–dominated reference stands, to 45 m inside adjacent younger, second-growth stands. The average ages of the latter were 6.0 years (regeneration), 27 years (sapling), 57 years (young forest), and 85+ years (mature forest). Diversity of EM was measured in soil cores sampled at five stations along each transect.

A total of 83 EM taxa were found. The most common taxa were *Cenococcum geophilum, "Pseudotsugaerhiza baculifera", Rhizopogon vinicolor,* and *Piloderma fallax*. Analyses of variance and covariance showed that species richness and proportion root colonization were drastically reduced with increasing distance from reference stands.

The reduction was smaller for the transitions from reference stand to sapling stands, and insignificant in transitions to young or mature regenerating forest. Despite the full recovery of EM abundance to pre-harvest levels, which occurred approximately 55 years after replanting, differences in community composition remained after 60 years. Future studies should examine particular host-species and also mixed host-species scenarios that could accelerate the recovery process.

Silvicultural practices aimed at promoting the re-establishment of EM fungi would include prompt replanting of harvested sites, using small cut-block sizes, minimal destruction of the forest floor, and green-tree retention.

Key words: fungal re-colonization, ectomycorrhizal ecology, Douglas-fir rotation age, old-growth forests, forest chronosequence, ecotone, diminished edge effects, ectomycorrhizal morphotypes

Résumé

L'objectif de cette étude était de déterminer l'influence des refuges sur le taux de récupération en matière de diversité ectomycorhizienne (EM) dans les zones de coupe à blanc et les forêts replantées en douglas de Menzies *(Pseudotsuga menziesii)* de la Colombie-Britannique, au Canada. Des transects ont été réalisés en deux endroits de la partie Sud de l'Île de Vancouver : Northwest Bay et Koksilah. Les transects partaient de 15 m à l'intérieur des peuplements de référence dominés par les derniers douglas de Menzies âgés de 90 ans et plus et les vieux douglas de Menzies, et s'étiraient jusqu'à 45 m à l'intérieur des peuplements secondaires plus jeunes adjacents. L'âge moyen des spécimens du peuplement secondaire était respectivement de 6 ans (régénération), 27 ans (gaulis), 57 ans (jeune peuplement) et 85 ans et plus (peuplement mûr). La diversité EM a été évaluée en prélevant des carottes dans le sol en cinq points répartis le long de chaque transect.

Au total, 83 taxa d'EM ont été relevés. Les taxa les plus communément relevés étaient *Cenococcum geophilum, « Pseudotsugaerhiza baculifera », Rhizopogon vinicolor* et *Piloderma fallax*. Les analyses de variance et de covariance ont montré que la diversité des espèces et l'importance de la colonisation du système racinaire diminuaient considérablement à mesure que l'on s'éloignait des peuplements de référence.

La réduction était moindre dans les zones de transition entre peuplements de référence et gaulis, et négligeable dans les zones de transition entre peuplements de référence et peuplements jeunes ou peuplements de régénération. En dépit du rétablissement complet de l'abondance des EM aux niveaux d'avant la récolte (rétablissement accompli environ 55 ans après la replantation), des différences dans la composition des communautés étaient encore observables au bout de 60 ans. De futures études devraient étudier certains hôtes particuliers, ainsi que les scénarios d'association d'hôtes susceptibles d'accélérer le processus de rétablissement.

Diverses pratiques sylvicoles pourraient contribuer à promouvoir le rétablissement de champignons EM, notamment : replantation rapide des sites ayant fait l'objet de coupes, zones de coupe réduites, destruction minimale du tapis forestier, ou encore réserve sur coupe.

Mots clés : colonisation fongique, écologie des ectomycorhizes, âge de rotation des douglas de Menzies, forêts anciennes, chronoséquence forestière, écotone, effets lisière diminués, morphotypes EM

1. Introduction

Worldwide, almost all conifer trees rely on mutually beneficial relationships between their feeder roots and certain types of soil fungi. These formations are known as ectomycorrhizae (EM) and play an important role in nutrient-cycling and protecting host trees from drought and disease. Douglas-fir ***(Pseudotsuga menziesii*** [Mirb.] Franco***)***, a dominant tree species in coastal British Columbia, is one example of a conifer known to form such symbioses. EM associations in Douglas-fir comprise nearly 2000 different fungi species. Most EM species require continuous presence of a live host in order to survive. Therefore, they are an important component of biodiversity and a useful indicator for assessing the potential deleterious effects of timber harvesting (Franklin et al. 1997; Kremsater et al. 2003). As forest practices evolve and change, so should our knowledge and decision-making with regard to the protection of key elements in these ecosystems; increasingly, these elements are stressed by human impacts and changing climate.

In our previous work, we investigated changes in ectomycorrhizal populations in variable retention (VR) systems (Outerbridge et al. 2001, unpublished report; Outerbridge and Trofymow 2004). This new silvicultural approach, an alternative to traditional clear-cut harvesting, was introduced in British Columbia in the late 1990s (Beese et al. 2003; Bunnell and Dunsworth 2009). We found clear evidence of edge effects in VR sites, with significantly lower abundance and diversity of EM fungi with increased distance from the retained forest patches. In another study near Powell River, British Columbia, we showed that EM richness and abundance in regenerating cutover areas adjoining mature forest were positively correlated with levels of green tree retention (Outerbridge and Trofymow 2009a).

In this study, we take the next step: we examine how the EM fungi associated with retained trees re-colonize a regenerating forest through time, by studying different ages of the reforested matrix.

Ectomycorrhizal growth, dispersal, and colonization patterns have been investigated in various studies (Carroll and Wicklow 1992), with particular focus on sites with forests regenerating after fire (Baar et al. 1999; Bruns et al. 2002; Jonsson et al. 1999; Stendel et al. 1999; Visser 1995). It has been estimated that mycelium travels through the forest floor at the rate of a few decimetres a year (Fiore-Donno and Martin 2001). Bradbury et al. (1998) found that 75% of the taxa present in undisturbed 90-year-old stands were colonizing the roots of adjacent regenerating lodgepole pine ***(Pinus contorta)*** in 10-year-old and 19-year-old cut blocks. Other studies, however, cite definite successional changes in forest fungi communities, caused either by the aging trees or by changes in the soil after harvesting (Dighton and Mason 1985; Keizer and Arnolds 1994; Norvell and Exeter 2004).

In this study we addressed several questions:

1. Assuming that retained forest patches serve as refugia for EM fungi, and assuming that these refugia create an edge effect at the tree line/clearcut boundary with regards to the abundance and diversity of EM fungi (Outerbridge and Trofymow 2004; Jonsson et al. 1999), how quickly do EM fungi re-colonize the adjoining reforested areas?

2. Are there any changes to the species composition?

3. Do the reforested areas assume the pre-harvest level of EM fungi with time?

4. What is the optimum rotation age of Douglas-fir stands for maintaining the pre-harvest biodiversity of EM fungi on Vancouver Island?

We hypothesized that all measurements of EM fungal diversity on new-growth Douglas-fir trees would return to pre-harvest levels within approximately 60 years from timber harvesting, given small cut-block size, prompt reforestation, and immediate adjacency of old-growth or mature forest.

2. Materials and methods

2.1 Sites description and establishment of forest age-transition transects

Twelve sites with previous research history were used to establish 12 transects in two areas of southern Vancouver Island: the Northwest Bay Operation area (NWB), located at 49.2811 N latitude and 124.2483 W longitude, and Koksilah (KOK), located at 48.6570 N latitude and 123.7530 W longitude (Table 1). This region is characterized by cool dry summers and mild wet winters; the sites spanned two biogeoclimatic zones from the Coastal Douglas-fir zone (CDF) in NWB, to the montane moist Coastal Western Hemlock maritime zone (CWH mm2) in KOK (Green and Klinka 1994). Soil type ranged from a very stony, rough, mountainous land series in KOK and NWB, to a brown podzolic type (loamy sand and/or gravelly loamy sand), or a concretionary brown type (gravelly sandy loam) at some sites at NWB (Day et al. 1959). The NWB sites are located at low elevation (< 300 m); the KOK sites are at higher elevation (circa 700 m). All of the stands were of natural fire origin or historically received some type of prescribed-burning treatments. Both areas are in privately managed forest land, formerly under the tenure of the Weyerhaeuser Coastal British Columbia Group, but as of 2006 in the tenure of Island Timberlands.

To assess the extent of EM re-colonization in recently harvested Douglas-fir forests, nine linear transects were established at nine sites in NWB, where one end of each transect was located in a mature, second-growth reference stand and the other end was located in stands at various stages of reforestation. There were three sites (1 transect at each site) corresponding to each stage of reforestation: ~6.0-year-old regeneration stands, 27-year-old sapling or pole stands, and 57-year-old young forest stands (Table 1; Figure 1). All transects extended from 15 m inside the reference stands to 45 m within the reforested areas. Sampling stations were established at –15 m, 5 m, 15 m, 25 m, and 45 m, where 0 m corresponds to the ecotonal boundary between a reference stand and the reforested area. At all of the stations, two soil cores (5 cm wide, 15 cm deep) were taken from within 1 m of a tree (Figure 1).

A similar experimental approach was applied for soil cores taken at KOK, where the reference stand was an old-growth stand previously studied by Goodman and Trofymow (1998). At KOK, transects (one at each of the three sites) extended from the reference stand into one of three reforestation stages: regeneration (5.0-years-old), young (57-year-old) and mature (85-year-old) stands. This provided a total of four age-transition types for the study (Table 1; Figure 1).

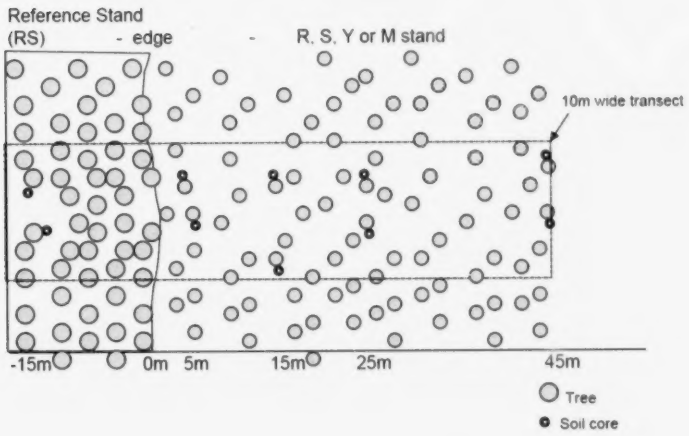

Figure 1. Experimental layout of transects and sampling stations at Northwest Bay and Koksilah.

R = regeneration stand, S = sapling/pole stand, Y = young stand, M = mature/old growth reference stand.

Table 1. Northwest Bay and Koksilah stand age-transition transect sites.

Reference stands *(RS)* were either mature (90- to 100-year-old) or old-growth (200+-year-old) forests.

Site (transect) #	Site research history	Stand age transition	Number of soil cores
	RS to regenerating clear-cut stands (R)		
NWB #1192	Carabid Beetle	100 yr → 8 yr	10
NWB #1193	Carabid beetle, Bryophyte	100 yr → 5 yr	10
NWB #1200	Bryophyte	90+ yr → 5 yr	10
Koksilah # 24	Chronosequence study	200+ yr → 5 yr	10
	RS to sapling/pole stands (S)		
NWB #1198	Bryophyte	90+ yr → 27 yr	10
NWB # 1204	Bryophyte	90+ yr → 27 yr	10
NWB #1199	Bryophyte	90+ yr → 27 yr	10
	RS to young forest stands (Y)		
NWB #1152	Carabid beetle	96 yr → 57 yr	10
NWB #1188	Bryophyte	90+ yr → 57 yr	10
NWB #1203	Bryophyte	90+ yr → 57 yr	10
Koksilah # 24	Chronosequence study	200+ yr → 57 yr	10
	RS to mature forest stand (M)		
Koksilah # 24	Chronosequence study	200+ yr → 85+ yr	10
TOTAL			120

2.2 Sampling and laboratory processing of soil cores

All soil cores were sampled in April (2005 in NWB; 2006 in KOK), stored at 2° C, and processed over the course of several months according to the methods of Goodman (1995). Soil plugs were gently washed with sieves to remove soil and debris. The washed root material from each core was placed in distilled water in a grid-lined plastic tray. The root pieces were randomly dispersed and, following the gridlines, all of the root tips from each core were examined for the presence of EM. This consistent method ensured that differences both in the numbers of roots contained in a soil core and in the morphotypes found were a reflection of treatment effects.

The following categories were quantified: dead roots; non-mycorrhizal roots; mycorrhizal roots; and individual EM morphological types (morphotypes). EM morphotypes were identified with the aid of a stereo-microscope. Observations of some cellular structures were made using a compound microscope under 400 X magnification and 1000 X oil immersion. Morphotypes were labeled according to colour or a set of distinguishing morphological features. Some morphological types were later identified to the genus or species level using methods described in Goodman et al. (1996–2009), Agerer (1987–2002, 1996–2002), and Ingleby et al. (1990), and for many of the morphotypes by DNA analysis (Egger et al. 2009; Baldwin et al. 2009). Two-page descriptions (photoprofiles) were created for all the EM morphotypes named in this study. These were added as links to the online *Ectomycorrhizae Descriptions Database* (EDD; BCERN 2008), a more recent version of the previous *Database of Descriptions of Ectomycorrhizae* (DDE; Goodman et al. 2000). For reference and future use and DNA analysis, root tips with representative morphotypes were preserved as voucher specimens in sterile water at –80°C.

2.3 Statistical analysis

Richness was defined as the number of EM morphotypes colonizing live root tips per soil core (sample). Total richness refers to the number of EM morphotypes per site. The proportion of root colonization was measured for each soil core, and calculated as the number of root tips colonized by one or more EM fungi, divided by the total number of live root tips examined. For particular morphotypes, proportional frequency refers to the proportion of occurrence versus all colonized root tips.

Replicate age-transition transects were not available for the KOK location as they were for the NWB location, and thus KOK data could not be included in the full analysis. However, three reference stands were measured at KOK, and as a supplementary analysis, we compared the EM diversity among all four groups of reference stands using analysis of variance with the general linear modeling (GLM) procedure in SAS STAT (SAS Institute 2007). The Tukey multiple comparison test was used to detect differences among means (SAS Institute 2007).

For the three forest age-transition types at NWB, the richness and the proportion root colonization from the distal reference-stand station to the 45 m station was investigated using the analysis of covariance component of the GLM procedure in SAS STAT (SAS Institute 2007). Distance along transect was used as the covariant and forest age-transition type was used as a class effect. Residuals were distributed normally, with α=0.05. Statistical analysis was not possible for the three forest age-transition types at KOK, as only one site per age transition was available.

3. Results

3.1 Ectomycorrhizal morphotypes and their frequencies

A total of 83 EM morphotypes, here also referred to as EM types, were detected along transects. Of those, 54 were in soil cores collected from NWB and 51 were found at KOK sites. Twenty-three EM types were common to both locations. Most taxa have not been identified and are referred to by code acronyms (in a couple of instances, Latin binomial code names, previously used in literature, were cited within quotation marks to distinguish them from the officially accepted fungal species names; see Table 2). This method is widely practiced (Agerer 1991; Jones et al. 1997; Wurzburger and Bledsoe 2001; Menkins 2005), and allows for comparative studies of EM despite the scarcity of knowledge concerning their taxonomic status. DNA analyses resulted in identification of some of the morphotypes to the species or genus level. Selected species or unidentified taxa from this study are also accompanied by photoprofiles or more detailed descriptions; these were entered into a database established for EM research in British Columbia (EDD; BCERN 2008; Table 2; Appendix A).

Overall, EM colonization of live roots was higher at KOK (83%) versus NWB (71%). The average level of live-root colonization by EM, based on all 12 sites, was 77%.

At NWB, 21 EM types (almost 40%) had proportional frequency of occurrence equal to 1% or higher, and the remaining 33 types were 'rare'. Among the common ones, ***Cenococcum geophilum***, ***"Pseudotsugaerhiza baculifera"***, and ***Rhizopogon vinicolor*** were most prevalent, accounting for 30.18%, 13.94%, and 9.95% of all EM root colonization, respectively (Table 2). At KOK, 16 EM types (31%) had proportional frequency of occurrence higher than 1%, and 35 morphotypes (almost 70%) were 'rare'. The top three were: ***"Pseudotsugaerhiza baculifera"*** (23.03%), ***Cenococcum geophilum*** (21.42%), and an unknown EM type, Copper (9.52%; see Table 2).

Table 2. Ectomycorrhizal morphotypes and their proportionate frequency of colonization (percent of all colonized root tips). See Appendix A for EM morphotype ID information.

EM morphotype collection name	Percentage of EM root tips colonized by morphotype	
	Northwest Bay	*Koksilah*
Ambys	1.72	1.0
AngelHL		3.9
BicolWhBr	0.09	
BlkBrLth		2.1
BlkBrPub	0.57	0.3
BlkPkMoz		0.2
BlkSndp		0.9
Blkwarty	1.60	
BlkWhPtch		0.5
BluBr	0.74	
BluMet		0.0
BluRhiz-L		0.3
BluYtip	0.28	
BrilCrO	0.95	0.03
BronzCont	0.04	
BrVerCor	0.52	0.32
BrVerShiny-L	0.06	
Canth		0.86
Ccaerules-L		1.60
Ccibar-L		0.29
CD14-like	0.21	3.15
Cenoc.	30.18	21.42
ChBrFuzSc	0.50	
Chlkptch	0.22	0.61
ClassicOpApx		0.07
ContpPchY	1.61	
Copper	1.19	9.52
Copper-LBr		1.05
CorPchWhBlm	3.38	
DrtypYcot	0.74	
GolPub	0.11	
GolYspgytor	0.64	0.9
GYBwoven	0.09	0.15
HonVelv	4.18	0.17
Humaria-L	0.36	
LacLuc-like	0.05	
Lactarub	2.02	3.00
Lactluc		0.18
LilPubBlRh		0.15
LimeBlk		0.07
MetGray		0.04
MicBrtoBkCor	1.04	
NtmegBrHon	0.55	
NtmegIvor	1.76	0.06
OLdkhy	0.57	
Orgroup		0.21
OrWptchSilk	0.17	
Pbaculi	13.94	23.03
PchFuzMptoCor	1.51	
PchWSc		0.19
PeachYcor		1.02
pGBrtoBrFVer	0.08	
Pilo	2.08	5.40
pOrCotMinrl		3.21
pYBfeltSc	1.07	
PYBrFuzWhRh	0.05	
pYfeltBrbase	0.30	0.97
pYShDichot	3.94	0.08
Rdens-like	0.52	
Rhizop	9.95	7.90
RustCotWh	0.72	
SalmFanMet	0.03	0.76
ShpYWhRh	0.05	
ShWcotY		0.18
Thick Rus		0.03
ThickYel	0.39	
ThTrPyr	0.07	0.08
TnWovOrBk	0.10	
Toment-like		0.07
Trunc	0.16	0.35
TrWhFeathr		0.87
TrWrefSlkRh		0.22
WaxSilW	0.77	
Wcott		0.50
WhFeathRh	1.04	
Whfeltdkbase	2.04	
WhOldSnow	0.11	
WhPeach		1.60
WHphob	3.05	
WhUnram		0.14
WYBsm	1.85	0.21
Ybmetcot	0.07	
YtBrick		0.15

3.2 Reference stands

The ANOVA analysis showed mean richness was not significantly different among the four groups of reference stands (Tables 3a and 4a), although overall it tended to be higher at KOK than at NWB. Total richness and proportion of roots colonized by EM fungi differed significantly among reference stands (Tables 3b, c and 4b, c), again with higher values in KOK reference stands.

Table 3. Analysis of variance for differences among reference stands at 15 m inside stand.

a) Mean EM richness is not significantly different among reference stands;

Source	R^2	*DF*	Sum of Squares	Mean Square	*F*	*Pr > F*
Model (Ref Stand)	0.57	3	26.1667	8.7222	3.52	0.0687
Error		8	19.8333	2.4792		
Corrected Total		11	46.0000			

b) Mean total EM richness is significantly different among reference stands

Source	R^2	*DF*	Sum of Squares	Mean Square	*F*	*Pr > F*
Model (Ref Stand)	0.64	3	92.0000	30.6667	4.84	0.0331
Error		8	50.6667	6.3333		
Corrected Total		11	142.6667			

c) Mean proportion of roots colonized by EM fungi is significantly different among reference stands.

Source	R^2	*DF*	Sum of Squares	Mean Square	*F*	*Pr > F*
Model (Ref Stand)	0.70	3	0.0607	0.0202	6.10	0.0183
Error		8	0.0265	0.0033		
Corrected Total		11	0.0873			

Table 4. Ectomycorrhizal fungi richness and abundance in reference stands

Means sharing the same letter (Tukey mean separation test) are not statistically different from each other.

a) Mean EM richness

Reference Stand	*N*	Mean	Std. Err.	Tukey Grouping
KOK	3	8.67	1.36	A
NWB_R	3	7.00	0.57	A
NWB_Y	3	5.50	0.58	A
NWB_S	3	4.83	0.88	

b) Mean total EM richness

Reference Stand	*N*	Mean	Std. Err.	Tukey Grouping
KOK	3	13.67	2.33	A
NWB_R	3	9.67	0.88	A B
NWB_Y	3	7.67	0.33	A B
NWB_S	3	6.33	1.45	B

c) Mean proportion of roots colonized by EM.

Reference Stand	*N*	Mean	Std. Err.	Tukey Grouping
KOK	3	0.85	0.01	A
NWB_S	3	0.83	0.03	A
NWB_R	3	0.79	0.02	A B
NWB_Y	3	0.67	0.05	B

N = number of sites

3.3 Effects of forest age on richness and root colonization

The ANCOVA analysis of the NWB mean richness data showed significant interaction between distance along transect and forest age-transition (Table 5a). As distance from mature stands increased, richness dropped most steeply in regenerating stands, and remained unchanged in sapling and young transition stands. The relatively low R^2 value indicated that factors other than stand age and transect position must also affect species richness. Additional regression analyses showed a second-order polynomial was a better fit (higher R^2) for the sapling and young age transitions but not for the regeneration. A broad peak in richness occurred from 5 m to 15 m in the sapling and young age transitions (Figure 2).

Total richness at NWB differed significantly among stations, but no significant differences were found among forest age transitions (Table 5b). Although the interaction between distance and forest age-transition was marginally insignificant (P=0.0660), and therefore might be significant with more data and lower variation, the trend in the interaction was similar to that described for mean richness.

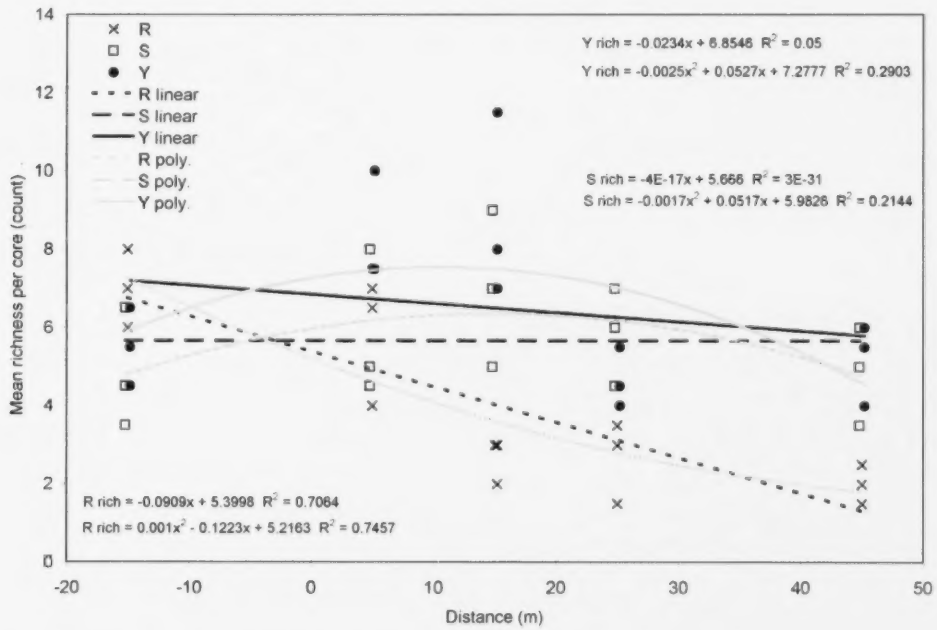

Figure 2. Ectomycorrhizal richness at Northwest Bay in three forest age-transition comparisons:

Transects were from 15 m inside mature (90+ years) reference stands to 45 m into adjacent planted forest stands of average age 6.0 years (regeneration – R), to 27 years (pole sapling – S), to 57 years (young forest – Y) (total *n*=45). There was significant interaction between distance along transect and forest age (P=0.0192). Graph shows the analysis of covariance-fit linear equations and line (black) for each age-transition type overlaid on the raw data. Complete model R^2=0.46 (P=0.000200). Fit of polynomial regression also shown (gray lines, lower equations).

For mean proportion of roots colonized, there was significant interaction between distance along transect and forest age-transition (Table 5c). The mean proportion of colonized roots dropped most steeply in regenerating stands with increasing distance from the mature stands, whereas it dropped less steeply in transects spanning mature stands and adjacent sapling stands, and increased slightly in the transects spanning mature stands and adjacent young forest. Additional analyses showed the second-order polynomial regressions fit no better than the linear regressions for all three age transitions (Figure 3).

As noted above, only one replicate of each forest age transition was measured at KOK and therefore could not be included in the formal analyses. Nevertheless, the pattern of interest observed at KOK was that of drastic decline (16-fold) in total richness from the old-growth reference stand to the regeneration area as distance increased from the reference stand. In contrast, measurement of the transect from the old-growth reference stand into adjacent mature forest (85+-year-old trees) provided random patterns along the whole transect, possibly signifying that total richness had recovered in the mature stand (data not shown; similar to Figure 2).

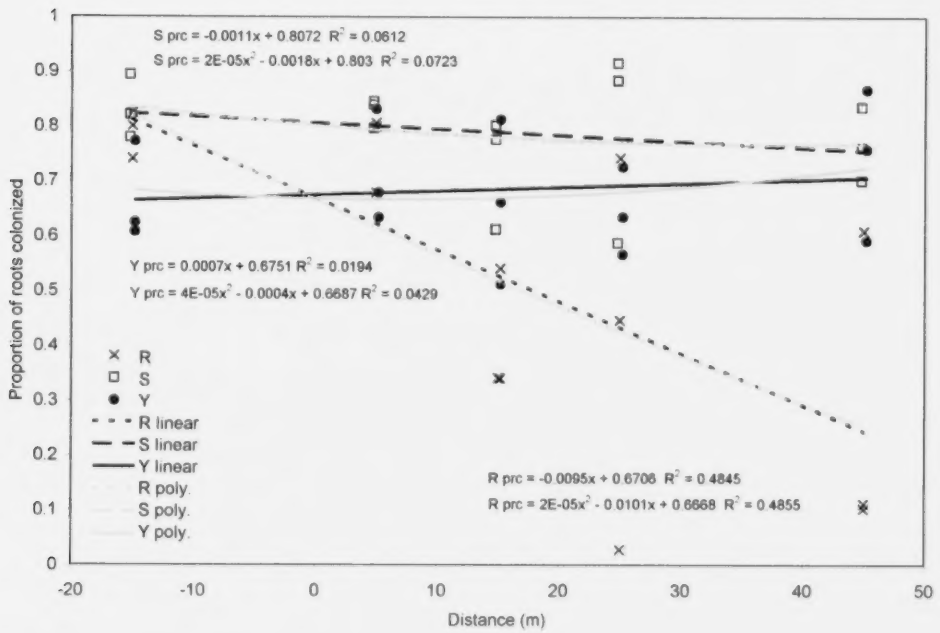

Figure 3. Proportion of roots colonized by ectomycorrhizal fungi at Northwest Bay

Transects were in three forest age-transitions: from 15 m inside reference mature stand (90+ years) to 45 m into adjacent planted forest stands of average age 6.0 years (regeneration – R), to 27 years (pole sapling – S), to 57 years (young forest – Y) (total n=45). There was a significant interaction between distance from stand edge and forest age (P=0.0010). Graph shows the analysis of covariance-fit linear equations and line (black) for each age-transition type over[illegible]d on the raw data. Complete model R =0.56 (P<0.0001). Fit of polynomial regression also shown (gray lines, lower equations).

Table 5. Analysis of covariance for differences in ectomycorrhizae diversity from 15 m inside reference stands to 45 m into adjacent younger stands ranging in average age from ~6.0 years to 57 years old.

a) Mean EM richness

Source	R^2	*DF*	Type III SS	Mean Square	*F*	*Pr > F*
Model	0.46	5	100.00	20.00	6.57	0.0002
Distance (D)		1	26.07	26.07	8.56	0.0057
Forest Age (A)		2	11.48	5.74	1.88	0.1654
D x A		2	26.70	13.35	4.38	0.0192
Error		39	118.80	3.05		
Corrected Total		44	218.80			

b) Mean total EM richness

Source	R^2	*DF*	Type III SS	Mean Square	*F*	*Pr > F*
Model	0.39	5	218.14	43.63	5.17	0.0010
Distance (D)		1	60.09	60.09	7.12	0.0110
Forest Age (A)		2	36.29	18.15	2.15	0.1300
D x A		2	49.21	24.61	2.92	0.0660
Error		39	329.10	8.44		
Corrected Total		44	547.24			

c) Proportion of roots colonized by EM

Source	R^2	*DF*	Sum of Squares	Mean Square	*F*	*Pr > F*
Model	0.56	5	1.0776	0.2155	9.95	<0.0001
Distance (D)		1	0.1934	0.1934	8.92	0.0048
Forest Age (A)		2	0.1180	0.0590	2.72	0.0783
D x A		2	0.3572	0.1786	8.24	0.0010
Error		39	0.8452	0.0217		
Corrected Total		44	1.9228			

** Note: Sum of Squares for Distance, Forest Age, and D x A are type III SS; others are type I SS.*

3.4 *Ectomycorrhizae total richness patterns and species composition*

In all transects spanning mature stands to regeneration age transitions, total richness in the latter was significantly reduced, in a pattern typical of a forest versus clear-cut boundary (Outerbridge and Trofymow 2004). In contrast, in all sites with transitions from mature forest to saplings or to young forest, or from old-growth forest to mature forest, the most frequent pattern of total richness was: -15 m < 5 m and/or 15 m > 25 m to 45 m. In other words, the total number of species was intermediate in the reference stands, high close to reference-stand edges, and lowest away from reference stands. As noted previously, this was similar to the results noted for the polynomial regressions of mean richness (Figure 2). Combining all –15 m and 5 m stations (i.e., the stations with the greatest mature- or old-tree influence) and contrasting them with the combined two stations furthest from the reference stands (25 m and 45 m) sheds additional light on the effects of forest age on species distribution (Table 6). At NWB, 11 of the 21 common EM fungi were found in higher numbers inside or at the edge of the older reference forest (at –15 m and/or 5 m stations) than at the distal portion of transects in the younger regrowing forest (at 25 m and/or 45 m stations). These morphotypes were HonVelv, WHphob, Pilo, Wybsm, Copper, pYBfeltSc, BrilCrO, pYshDichot, Ntmeglvor, Ambys, ContPchY, with the last four types possibly emerging as ecotonal 'edge specialists' - those preferring to grow near forest edges. In contrast, only one of the common EM types was found exclusively in the regeneration stand (Wfeltdkbase), and two (WhFeathRh, MicBrtoBkCor) were found in higher numbers in the younger forest than in the older reference forest.

Four EM types (Cenococ, Rhizop, Lactarub, PchFuzMptoCor) showed no clear preference for habitat, and three (Pbaculi, CorPchWhBlm, Blkwarty) had rather patchy distribution. Among the 35 'rare' fungi at NWB, 14 types were found exclusively or in higher numbers at –15 m and/or 5 m stations compared to 25 m and/or 45 m stations. Only nine EM types showed the reverse pattern.

At KOK, five of the 16 common EM types were found in higher numbers inside or at the edge of the reference old-growth forest (at –15 m and/or 5 m stations) compared to the younger cut blocks (at the 25 m and/or 45 m stations). These morphotypes were: AngelHL, pOrCotMinrl, Ccaerules-L, WhPeach, PeachYCor. Two common EM types from the cutblocks, Ccibar-L and PYFeltBrBase, were not found at either the –15 or 5 m stations, and Lactarub and Ccibar-L were at their highest frequency at the 45 m station. The other common EM types, such as Pbaculi, Cenoc, Copper, Rizop, Pilo, and Ambys, had either patchy or fairly uniform distributions along transects. Comparison of 35 'rare' species from the pooled three sites at KOK showed higher total richness in old-growth reference stands compared to their adjacent ecotonal areas. Twenty-one EM types were not found at either the 25 m or 45 m stations, and 11 were absent from either the –15 m or the 5 m stations. Due to the low numbers of roots colonized by the rare fungi, the significance of their occurrence in older versus younger forests remains unresolved and requires further study.

Table 6. Overall proportional frequency of the most common ectomycorrhizal types at Northwest Bay and Koksilah, and corresponding number of colonized root tips for each ectomycorrhizal type from pooled stations: -15 m and 5 m versus 25 m and 45 m.

Frequency (%)	EM morphotype code	Colonized root tips Sum -15 m to 5 m	Colonized root tips Sum 25 m to 45 m
	Northwest Bay		
30.2	Cenoc	4005	4192
13.9	Pbaculi	2257	1654
9.9	Rhizop	1285	1286
4.2	HonVelv	1263	198
3.9	pYShDichot	588	177
3.4	CorPchWhBlm	714	463
3.0	WHphob	1068	0
2.1	Pilo	559	9
2.0	Whfeltdkbase	0	687
2.0	Lactarub	146	513
1.9	WYBsm	541	87
1.8	Ntmeglvor	572	0
1.7	Ambys	566	0
1.6	ContpPchY	433	123
1.6	Blkwarty	80	468
1.5	PchFuzMptoCor	283	246
1.2	Copper	410	0
1.1	pYBfeltSc	375	0
1.0	WhFeathRh	0	363
1.0	MicBrtoBkCor	0	363
0.9	BrilCrO	325	0
	Koksilah		
23.0	Pbaculi	927	208
21.4	Cenoc	943	707
9.5	Copper	157	532
7.9	Rhizop	401	176
5.4	Pilo	366	29
3.9	AngelHL	284	0
3.2	pOrCotMinrl	251	11
3.2	Ccibar-L	0	228
3.0	Lactarub	48	162
2.1	BlkBrPub	58	91
1.6	Ccaerules-L	116	0
1.6	WhPeach	116	0
1.1	Copper-LBr	55	21
1.0	PeachYcor	56	0
1.0	Ambys	69	28
1.0	PYFeltBrBase	0	70

4. Discussion

Other researchers have pursued the topic of EM fungi in the context of forest-age comparisons. Bradbury et al. (1998) studied EM succession in regenerating lodgepole pine adjacent to 90-year-old undisturbed stands. They report a total of 43 taxa, with *"Mycelium radicis-atrovirens"* being the most common associate. *Cenococcum geophilum* and species of *Piloderma, Suillus, Lactarius* and *Russula*-like were also prevalent. The control plots yielded 20 different mycorrhizal taxa, of which 13 were found in 6-year-old cut blocks, and 15 were found in 10- and 19-year-old cut blocks. The researchers found no evidence of succession in the EM fungal communities. Goodman and Trofymow (1998) found no difference in EM abundance or richness between old-growth and mature stands immediately adjacent to each other, but did not investigate other age transitions. Smith et al. (2000) reported on distribution of *Piloderma fallax* in young, rotation-age and old-growth stands of Douglas-fir in Oregon and provide a good overview of literature on the subject. Smith et al. (2002) investigated hypogeous and epigeous mycorrhizal fungal sporocarps of different forest-age classes. They found similarity in diversity among age classes but differences in species composition, as well as significantly lower EM sporocarp biomass in old-growth stands versus young and rotation-age stands. In a study by Visser (1995), both fruit body (50 species) and root assessments (39 EM types) revealed a distinct fungal succession following wildfire in jack pine stands. A significant increase in species richness occurred between 6-year-old and 41-year-old stands, at which point both the composition and structure of the mycorrhizal community had stabilized.

Although comparisons of forest stands of different ages are useful in general discussions on biodiversity, silvicultural impacts, or vegetation-related fungal successions, it is difficult to draw firm conclusions from such studies about the rate of regeneration of fungal populations following a disturbance. By incorporating stands of increasing ages adjacent to mature or old-growth forests in our experimental design, we attempted to observe a more dynamic system that could provide more direct evidence on the progress of EM re-colonization. The old-growth and mature reference stands served a dual purpose: to test our assumption that most of the pre-harvest EM fungi were lost or severely depleted at each site soon after clear-cut harvesting, and to provide the pre-harvest reference point appropriate for each site. Differences in the reference stands demonstrate the value in having an appropriate control when testing for age effects.

The results demonstrate great variability in the ability of EM fungi to re-establish reforested areas from adjoining refugia. It was not surprising to see a decline in total richness in the clear-cuts with increasing distance from the uncut forest, previously reported in literature (Kranabetter and Wylie 1998; Hagerman et al. 1999a; Durall et al. 1999; Outerbridge and Trofymow 2004). Equally expected was the resilience of several ubiquitous taxa, e.g., *Cenococcum* or *Rhizopogon*, sometimes classified as 'multi-stage' fungi or a resistant propagule community of EM fungi (Kranabetter 1999; Taylor and Bruns 1999). Affinities of various EM species for specific host-age classes have long been known (Dighton and Mason 1985). A higher production of sporocarps in mature forests versus younger or regeneration forests has been previously reported (Veijalainen 1976; Vogt et al. 1981; Amaranthus et al. 1994), although the reverse has also been noted (Jansen and Denie 1988). More importantly, however, our study indicates that EM diversity (here measured by observations of mean richness, total richness and proportion of roots colonized by EM) shows partial to full recovery after approximately 30 to 60 years since stand replacement. Our results are somewhat corroborated by a similar study (Twieg et al. 2007), wherein the diversity of EM fungi was observed to reach a plateau by the 26-year-old class, whereas community composition stabilized by the 65-year-old class. However, our results demonstrate only a quantitative recovery of diversity for EM fungi, whereas differences in community structure occurred along the mature versus young forest transects at Northwest Bay, and the old-growth versus mature forest transects at Koksilah. This means that, while certain unaffected EM fungi persist on harvested sites, other species are depleted or eliminated, and a long-term change in species composition occurs. The ability of the depleted or eliminated species to re-establish and expand would depend on their dispersal strategies, competitiveness, environmental influence, host–fungus relations, and other successional forces (Carroll and Wicklow 1992). When original stands are removed, disruption of existing fungi succession patterns and accompanying changes in soil properties occur. These conditions lead to fresh opportunities for surviving species, as well as for new invaders. Spores and other resistant propagules are the primary inoculum source for seedlings in regenerating forests (Baar et al. 1999). With time, hyphal advancement fills the void (Amaranthus et al. 1994). Some of the EM fungi in the adjacent retained forest are able to colonize younger trees, or perhaps even do so preferably, as their growth on the old trees slows down. Thus, temporal and spatial linkages are created among the seedlings in the cutblock, and also between the seedlings and the adjacent older forest.

The EM communities of a retained mature or old forest stand can shape EM fungal community structure of the forest in a regenerating cut block via legacy EM propagules and by providing a source of inoculum for vegetative recolonization processes. However, both mechanisms are clearly affected by factors and forces which allow changes in species composition to occur. Among these factors are timing of re-planting, host type and developmental stage, alteration of soil and microenvironment, animal–fungus relations, disturbance level, size of the disturbed area, and additional sources of inocula other than the immediately adjacent refugia (Fogel and Trappe 1978; Molina et al. 1992; Amaranthus et al. 1996; Hagerman et al. 1999b; Durall et al. 1999; Kranabetter and Kroeger 2001; Jones et al. 2003). Therefore, we can assume that in secondary succession of EM fungi, the process of re-colonization has two important dimensions: species recovery and species replacement. Both of these dimensions appear to be of critical importance in the overall drive to occupy all of the available niches.

Considering these results in concert with those of other studies, it appears that the abundance of EM niches is high inside the forest and sometimes highest at the forest edge, but decreases with distance from it (Durall et al. 1999; Outerbridge and Trofymow 2004). Also, the total richness of EM follows the low–high–low pattern, in that regeneration stands are species-depleted, but young forests (50 to 60 years old) frequently have higher EM diversity than mature or old-growth forests (Dighton and Mason 1985; Countess 2001; Smith et al. 2002).

Will the re-growing forests of Northwest Bay and Koksilah sites continue the upward trend in EM diversity? Will their ectomycorrhizal communities eventually resemble those currently found in the adjacent 90 to >200 years older forests? It is unfortunate that the time scales involved in many ectomycorrhizal research projects, as well as the complexities of forest origins, make it almost impossible to directly answer such questions.

At the sites used in this study, the full recovery of EM abundance to pre-harvest levels occurred approximately 55 years after replanting. Despite the quantitative EM recovery, differences remained in community composition after 60 years. These time scales for recovery processes seem plausible, considering the observations of Fiore-Donno and Martin (2001), who estimated a rate of several decimetres (y^{-1}) for mycelial advancement through forest floor. The cut blocks in our study were promptly replanted with seedlings, an action essential for conservation of EM inocula (Wiensczyk et al. 2002). Future studies should examine particular host-species and mixed host-species scenarios that may accelerate the recovery process.

Silvicultural practices aimed at promoting the re-establishment of EM would benefit from incorporating other known beneficial methods, such as small cut-block sizes, minimal destruction of the forest floor, and green tree retention (Hagerman et al. 1999a and b; Wiensczyk et al. 2002; Outerbridge and Trofymow 2004; Cline et al. 2005; Luoma et al. 2004).

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Appendix A

Morphotypes, their taxonomic identification, GenBank numbers and other publications, where available, for ectomycorrhizae (EM) collected from Douglas-fir roots during this study. The morphotypes listed without any information will have their photoprofiles completed as more EM root material becomes available.

EM morphotype collection name	Fungal Taxon ID or closest match*	GenBank number and author(s)	Other Publication	EM morphotype collection number
Ambys	***Amphinema byssoides***-like		Harniman and Durall 1996	NWBRO1
AngelHL	unidentified		PoE	KKSRO2
BicolWhBr	***Tomentella*** cf. ***sublilacina***	EU645641 (Outerbridge et al. 2008)**	PoE[1]	NWBRO2
BlkBrLth	Tomentella sp.	EU645597 (Outerbridge et al. 2008)**	PoE[1]	STIL2RO5
BlkBrPub	unidentified		PoE	KKSRO4
BlkPkMoz	unidentified		PoE in prep.	STIL2RO6
BlkSndp	***Thelephoraceae*** sp. * (91%)	AF274776.1 (Koljalg et al. 2000)*	PoE[1]	STIL2RO7
Blkwarty	unidentified		PoE in prep.	NWBRO4
BlkWhPtch	unidentified		PoE	KKS2RO4
BluBr unidentified	EU645637 (Outerbridge et al. 2008)**		PoE[1]	NWBRO5
BluMet	unidentified		PoE	KKS2RO6
BluRhiz-L	***Rhizopogon*** cf. ***parksii***	EU645618 (Outerbridge et al. 2008)**	PoE[1]	STIL2RO9
BluYtip	unidentified		PoE[1]	NWBRO6
BrilCrO	***Piloderma*** sp.	EU645645 (Outerbridge et al. 2008)**	PoE[1]	NWBRO7
BronzCont	***Thelephora*** sp.	EU645642 (Outerbridge et al. 2008)**	PoE[1]	NWBRO8
BrVerCor	***Thelephoraceae*** sp.		PoE[1]	KKSRO6
BrVerShiny-L	unidentified		PoE in prep.	NWBRO10
Canth	***Cantharellus*** cf. ***formosus***		PoE[1]	VR2RO7
Ccaerules-L	unidentified	EU645625 (Outerbridge et al. 2008)**	PoE[1]	KKS2RO27
Ccibar-L	unidentified		PoE	KKS2RO9
CD14-like	***Inocybe*** sp.	EU645638 (Outerbridge et al. 2008)**	PoE[1]	NWBRO11
Cenoc.	***Cenococcum geophilum*** Fr.	EU645646 (Outerbridge et al. 2008)**	PoE[2]	VR2RO8
ChBrFuzSc	***Thelephoraceae*** sp.	EU645643 (Outerbridge et al. 2008)**	PoE[1]	NWBRO13
Chlkptch	unidentified		PoE	KKSRO9
ClassicOpApx	unidentified		PoE	KKS2RO10
ContpPchY	***Sebacinaceae***	EU645626 (Outerbridge et al. 2008)**	PoE[1]	NWBRO15
Copper	unidentified		PoE	VR2RO9
Copper-LBr	***Cortinarius*** sp.	EU645624 (Outerbridge et al. 2008)**	PoE[1]	KKS2RO12
CorPchWhBlm	unidentified		PoE	NWBRO17
DrtypYcot	unidentified	EU645627 (Outerbridge et al. 2008)**	PoE[1]	NWBRO18
GolPub	unidentified		PoE[1]	NWBRO19
GolYspgytor	***Cortinarius*** cf. ***glaucopus***	EU645632 (Outerbridge et al. 2008)**	Outerbridge and Dennis 2009a	NWBRO20
GYBwoven	unidentified		PoE in prep.	KKSRO11
HonVelv	***Russulaceae*** sp.	EU645647 (Outerbridge et al. 2008)**	PoE[1]	NWBRO22
Humaria-L	***Wilcoxina*** cf. ***rehmii**** (99%)	AF266708 (Bidartondo and Bruns 2000)*	PoE[1]	NWBRO23

EM morphotype collection name	Fungal Taxon ID or closest match*	GenBank number and author(s)	Other Publication	EM morphotype collection number
LacLuc-like	unidentified		PoE in prep.	NWBRO24
Lactarub	***Lactarius rubrilacteus***		PoE[1]; Eberhart and Louma 1997	VR2RO16
Lactluc	***Lactarius*** sp.	EU645605 (Outerbridge et al. 2008)**	PoE[1]	KKSRO14
LilPubBlRh	unidentified		PoE	KKS2RO18
LimeBlk	unidentified		PoE	KKSRO15
MetGray	unidentified		PoE in prep.	KKSRO16
MicBrtoBkCor	unidentified		PoE	NWBRO26
NtmegBrHon	unidentified		PoE	NWBRO27
Ntmeglvor	***Inocybe*** sp.*(93%)	EF619710 (Outerbridge et al. 2008)**	PoE[1]	NWBRO28
OLdkhy	unidentified		PoE	VR2RO18
Orgroup	***Inocybe*** cf. ***pudica***	EU645621 (Outerbridge et al. 2008)**	PoE[1]	VR2RO20
OrWptchSilk	***Cortinarius cinnabarinus**** (93%)	AY669662 (Garnica et al. 2005)*	PoE[1]	NWBRO30
Pbaculi	***"Pseudotsugaerrhiza baculifera"***		Muller and Agerer 1996	VR2RO21
PchFuzMptoCor	***Cortinariaceae*** sp.	EU645628 (Outerbridge et al. 2008)**	PoE[1]	NWBRO32
PchWSc	***Russula*** cf. ***decolorans***	EU645607 (Outerbridge et al. 2008)**	PoE[1]	STIL2RO29
PeachYcor	inidentified		PoE	KKSRO19
pGBrtoBrFVer	***Thelephoraceae*** sp.		PoE in prep.	NWBRO33
Pilo	***Piloderma fallax*** (Libert) Stalpers	EU645648 (Outerbridge et al. 2008)**	PoE[2]; Goodman and Trofymow 1996	NWBRO34
pOrCotMinrl	***Sebacina*** sp.*(97%)	AF440652 (Selosse et al. 2002)*	PoE[1]	KKS2RO23
pYBfeltSc	***Basidiomycete***		PoE[1]	NWBRO35
PYBrFuzWhRh	unidentified			NWBRO36
pYfeltBrbase	inidentified			NWBRO37
pYShDichot		EU645629 (Outerbridge et al. 2008)**	PoE[1]	NWBRO38
Rdens-like	***Russula*** cf. ***brevipes***	EU645633 (Outerbridge et al. 2008)**	Outerbridge and Trofymow 2009b	NWNRO39
Rhizop	***Rhizopogon vinicolor***-like	EU645650 (as ***Rhizopogon*** sp.) (Outerbridge et al. 2008)**	PoE[1]; Goodman 1996	NWBRO40
RustCotWh	***Hebeloma saliciphilum, Hebeloma polare, Hebeloma atrobrunneum***	AY312986.1 (Zimdars, 2003), AY312977.1 (Zimdars, 2003), AY308586.1 (Zimdars, 2003)*	PoE in prep.	NWBRO41
SalmFanMet	unidentified		PoE	KKSRO24
ShpYWhRh	unidentified		PoE	KKSRO26
ShWcotY	unidentified		PoE	KKS2RO28

EM morphotype collection name	Fungal Taxon ID or closest match*	GenBank number and author(s)	Other Publication	EM morphotype collection number
Thick Rus	unidentified		PoE	VR2RO28
ThickYel	***Russula*** cf. ***occidentalis*** * (97%)	AY534206 (Horton et al. 2005)*	Outerbridge 2009	VR2RO29
ThTrPyr	***Piloderm*** sp.* 83%	DQ474736.1 (Wright et al.2006)*	PoE[1]	KKSRO27
TnWovOrBk	***Russula*** sp.* 82%	EF218807 (Twieg et al. 2007)*	PoE[1]	NWBRO46
Toment-like	***Inocybe pudica**** (86%)	AY228341 (Skogstad et al. 2003)*	PoE[1]	STILRO22
Trunc	***Truncocolumella citrina***		PoE; Eberhart and Luoma 1996	VR2RO33
TrWhFeathr	unidentified		sample missing	KKS2RO34
TrWrefSlkRh	unidentified		PoE in prep.	KKSRO34
WaxSilW	***Inocybe*** sp.	EU645639 (Outerbridge et al. 2008)**	PoE[1]	NWBRO48
Wcott	***Cortinarius*** sp.	EU645620 (Outerbridge et al. 2008)**	PoE[1]	STIL2RO47
WhFeathRh	***Ramaria*** sp.	EU645630 (Outerbridge et al. 2008)**	PoE[1]	NWBRO49
Whfeltdkbase	***Clavulina*** cf. ***cristata***	EU645631 (Outerbridge et al. 2008)**	Outerbridge and Dennis 2009b	NWBRO50
WhOldSnow	unidentified	EU645640 (Outerbridge et al. 2008)**	PoE[1]	NWBRO51
WhPeach	***Inocybe*** sp. (96%)*	EF218772.1 (Tweig et al. 2007)*	PoE[1]	KKSRO38
WHphob	***Phellodon*** cf. ***niger***	EU645613 (Outerbridge et al. 2008)**	PoE[1]	STIL2RO48
WhUnram	unidentified	EU645644 (Outerbridge et al. 2008)**	PoE[1]	KKSRO39
WYBsm	unidentified	EU645652 (Outerbridge et al. 2008)**	PoE[1]	NWBRO53
Ybrnetcot	***Pseudotomentella nigra**** (94%)	AF274770.1(Koljalg et al. 2000)*	PoE[1]	STILRO31
YtBrick	unidentified		PoE[1]	KKSRO41

** Samples not submitted to GenBank by the authors (due to taxonomic uncertainties), but tentatively identified based on a close match with an existing accession, as referenced by the appropriate GenBank numbers and the authors. For more information, search by GenBank number at:* ***http://www.ncbi.nlm.nih.gov/sites/entrez?db=nucleotide***

*** Outerbridge R.A.; Trofymow, J.A.; Durall, D. 2008. Direct submission to GenBank. For details of remaining citations, check the appropriate photoprofiles (search by EM collection number) in:* ***http://www.pfc.cfs.nrcan.gc.ca/biodiversity/bcern***

Appendix B:

Ectomycorrhizal sporocarp survey

As a side study, and to augment the soil core data, we carried out a sporocarp survey on the sites. We were specifically interested in whether the commercially important ectomycorrhizal macrofungi (EM), such as chanterelles (***Cantharellus*** spp.) or pine mushrooms (***Tricholoma magnivelare***), were present in any of the stands and if their communities might differ between the four forest age classes.

Sporocarps of epigeous EM fungi were surveyed twice, once in the spring and once in the fall of 2006, along the full transect length. They were identified to species or genus level using general specialized taxonomic literature, field guides and computer software [Matchmaker: Mushrooms of the Pacific Northwest (MMPNW; BCERN 2007)].

Sporocarps of eight edible EM found in the study could be classified as having existing or potential commercial value. The majority occurred at the Koksilah location. These were: ***Cantharellus formosus, Tricholoma magnivelare, Boletus mirabilis, Suillus lakei, Lactarius rubrilacteus, Sarcodon imbricatum,*** and ***Russula xerampelina***. In addition to *C. formosus, L. rubrilacteus,* and *R. xerampelina,* the Northwest Bay sites also yielded sporocarps of ***Craterellus tubaeformis.*** Sporocarps for all these species were found only in the mature or old-growth reference forest, with the exception of ***Lactarius rubrilacteus***, which was also found in the sapling forest. No statistical analyses were done or conclusions drawn as data were insufficient.

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